Notes on the Biology of *Stelis* (*Odontostelis*) *bilineolata* (Spinola), a Parasite of *Euglossa cordata* (Linnaeus) (Hymenoptera: Apoidea: Megachilidae)

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Abstract: The activities of the parasitic bee *Stelis* (*Odontostelis*) *bilineolata* (Spinola) in specially constructed box nests of its host *Euglossa cordata* (Linnaeus) are reported. The female enters the nest, forces the attendant *Euglossa* female to abandon the nest, and remains in the nest for several days. She opens those cells containing eggs or small larvae, seals, removes, and destroys them and after depositing her own egg reseals the cell. Cells with older stages of *Euglossa* are not opened but the larva or pupa contained therein is killed. Feeding behavior of the small and large larvae and construction of the cocoon are described.

During studies on the biology of *Euglossa* spp. in Trinidad some of the observation nests were invaded by the parasitic bee *Stelis* (*Odontostelis*) *bilineolata* (Spinola). It is planned to publish the results of the *Euglossa* studies separately when they are completed but it seems advisable at this time to publish a note on the activities of its parasite as a companion paper to one on the morphology of the immature stages by Rozen (1966).

NESTING HABITS OF *Euglossa cordata*

To explain the behavior of *S. bilineolata* it is necessary to describe briefly the nesting habits of *Euglossa*. Two species of this genus, *E. cordata* and *E. variabilis* (Friese),[2] which are solitary species, have been induced to nest in small wooden boxes (inside dimensions $10 \times 6 \times 4.5$ cm) with a 10-mm circular entrance hole on one side. Once a nest is occupied and cell construction started the wooden top can be replaced by a pane of glass through which activities within the nest can be readily observed.

The bee cements the glass lid to the wood with a brown resinlike plant material which is used to seal all cracks and joints on the inside of the box and also to close the entrance hole. When leaving the nest the female opens a smaller circular hole in the resin just large enough for passage. She never closes the entrance when leaving the nest, even when leaving for the last time, but always seals it in the evening and frequently during the day while working inside. Cells of the same resinlike material are constructed either on the floor of the box or on the side, usually each cell being provisioned and sealed before another is started.

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[2] Although all observations were in nests of *E. cordata* the parasite has also been reared from nests of *E. variabilis*.

Observations on the behavior of *Stelis*

When a *Stelis* adult was first noted in observation box No. 3[3] on July 12, 1964 neither its identity nor the significance of its presence was immediately appreciated. This nest which had been first occupied by *Euglossa* in April contained nine cells, some with immature stages, others from which adults had emerged, and a tenth cell only partially constructed and partially provisioned. Work on this cell stopped about July 4. It is probable that the bee was attacked by a conopid and, although still capable of flight, her ovaries had ceased to function. She was present in the nest with the intruder and on the bottom of the box there was also a small *Euglossa* larva. The *Stelis* frequently approached and nudged the *Euglossa* female with her mandibles; the latter kept turning away and finally retreated to a corner of the box. During the next 20 minutes the *Stelis* female spent most of the time examining the cell mass.

At 6:45 A.M. the following morning both adults were in the nest, the *Euglossa* in a corner and the *Stelis* on the cell mass. By 7:45 A.M. the *Euglossa* went out and the *Stelis* began to close the entrance from the inside. The larva on the floor was dead and partially covered with wax.

The box was examined from time to time on succeeding days and the presence or absence of the two bees noted. This information is summarized in Table 1. Although the *Stelis* female was frequently on the cell mass she did not open any of the cells during the periods of observation. The walls of two cells from which *Euglossa* adults had emerged a few days earlier were partially broken down by the *Euglossa* while the *Stelis* was either resting on the the side of the box or absent from the nest.

No further activity occurred in this nest when (due to my absence from Trinidad) observations were suspended on October 3. When I next examined the nest on December 6 a *Stelis* adult had emerged from one cell. The other cells when opened later contained dead pupae and mature larvae of *Euglossa*.

When observations on the box nests were continued in December it was evident that a number of other nests had been attacked, i.e., sealed cells present, no attendant *Euglossa* adult but the entrance sealed. This was confirmed later when *Stelis* adults emerged from one or more cells in these boxes.

On December 6, nest 12, which was started on September 30 but still retained its wooden cover, contained a dead *Euglossa* adult (parasitized by a conopid); a *Stelis* adult; three sealed cells with somewhat flattened walls, and a fourth partially completed cell. When examined on December 8 the *Stelis* was absent (an adult, possibly the same one, was present in nest 13) but was in again on December 9 and 10. On December 11 the wooden top was replaced by a sheet of glass and by December 12 the *Stelis* utilizing bits of resin present in the box had sealed the glass in place in a manner similar to *Euglossa*. Although out

[3] The boxes were numbered serially as they were occupied by *Euglossa*.

TABLE 1. Records of the presence of *Euglossa* and *Stelis* in the nest during periods of observation.

Date and time of observation		*Euglossa*	*Stelis*	Entrance hole
July 12	7:30 A.M.	In	In	Closed
July 13	6:45 "	"	"	"
	7:45 "	Out	"	Being closed
	12:10 P.M.	In	Out	Closed
	1:20 "	"	In	"
	5:45 "	"	"	"
July 14	7:20 A.M.	"	"	"
	1:05 P.M.	"	"	"
	4:05 "	"	"	"
July 15	7:30 A.M.	"	"	Open
	5:15 P.M.	"	"	Closed
July 16	7:45 A.M.	"	"	"
	12:15 P.M.	"	Out	"
	5:05 "	"	"	"
July 17	7:30 A.M.	"	"	"
	11:45 "	Out	Out	"
	12:45 P.M.	"	"	"
	4:45 "	"	"	"
July 19	7:45 A.M.	"	"	"
	2:45 P.M.	Out[1]	In	"
	3:20 "	"	Out[2]	"
July 20	10:45 A.M.	In	"	"
	1:30 P.M.	Out	In	"
	4:45 "	"	"	"
July 21	7:50 A.M.	Out[3]	"	"
	1:40 P.M.	Out	Out[4]	"

[1] The *Euglossa* female, readily recognized by markings of enamel paint coding, was in a nearby nest abandoned a few days earlier by another female.

[2] The *Stelis* completing the closing of the entrance from the outside.

[3] Observed in an adjacent nest.

[4] Sealing the nest from the outside.

of the nest at 11:40 A.M. on the 12th (an adult was in nest 6 at this time) she returned on October 13 but was not seen thereafter. A week later the entrance of the nest was corked and on February 4 a *Stelis* adult emerged. The other two cells when opened later contained immature dead *Euglossa* pupae. As far as could be determined the cells had not beeen opened and the death of the occupants was apparently attributable to the actions of *Stelis,* i.e., killed either by mandibular crushing of the cell walls or by stinging.

Although a *Stelis* female was noted in a few other nests no further observations of consequence were made until January 24, when a female was observed in nest 9. First occupied by *Euglossa* in August, activity in this nest was suspended three times by the action of conopids: the original female, a succeeding daughter, and finally a parasitized granddaughter that died in the nest. The progeny of the last female emerged between December 9, 1964 and January 3, 1965. A

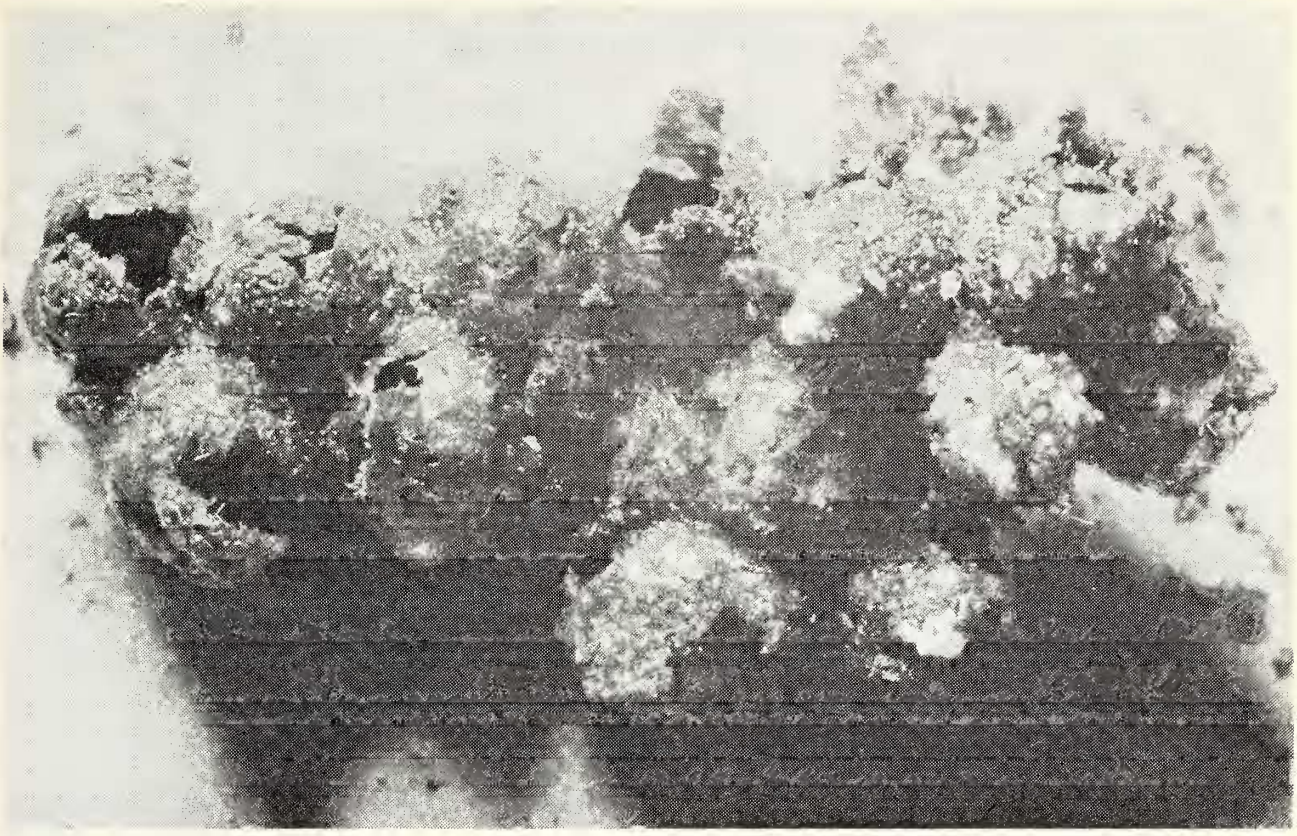

Fig. 1. Nest 9 of *Euglossa cordata* viewed from top. (Cells were opened for observations.) (Photo by J. Rozen.)

female emerging on December 26 remained in the nest. She reconditioned, provisioned, and sealed her first cell on December 31. By January 24 she had provisioned and sealed 12 cells and partially provisioned another when the nest was invaded by *Stelis* on the following day. When examined at 12:35 P.M. the *Euglossa* and a *Stelis* female were in the nest and the entrance closed. During the next 20 minutes the *Stelis* chased and grabbed the *Euglossa* in her mandibles and attempted to sting her on three occasions; each time the *Euglossa* broke free and retreated to a corner of the box. At 12:55 P.M. the *Euglossa* attempted to escape from the nest but before she could open the entrance was chased away by the *Stelis*. The *Stelis* then spent several minutes resealing the entrance. Further pursuit with repeated capture and apparent stinging occurred until finally at 1:09 P.M. the *Euglossa* managed to open the entrance and escape. Less than a minute later the *Stelis* was reclosing the opening. She then explored the walls of the box and approached the cell mass. When observations were resumed at 1:25 P.M., *Stelis* was opening the top of a cell which had been sealed 8 days earlier. By 1:30 P.M. the hole was enlarged enough to permit insertion of her head. She grasped the *Euglossa* larva contained therein (less than one-third grown), tugged it out of the cell, carried it to the front of the box, and dropped it on the floor. After biting and stinging it several times she returned to the cell, inspected it for a few seconds and for several minutes wandered about the box encountering and stinging the larva a number of

TABLE 2. Record of oviposition by *Euglossa* and *Stelis* female in nest 9.

Cell number	Date egg deposited by *Euglossa*	(a) Date egg deposited by *Odontostelis* (b) Contents of cell when opened on February 4
10	December 31	b Dead pupa (E)[1]
11	January 5	b Postdefecating larva (E)
12	" 7	b Prepupa (alive) (E)
13	" 10	b Postdefecating larva (E)
14	" 11	b " " " (E)
15	" 13	b Predefecating larva (E)
16	" 14	b Defecating larva (E)
17	" 17	a January 26
18	" 18	a " 26[2]
19	" 20	a " 27
20	" 22	a " 28[2]
21	" 24	a " 29
22	Provisioned only	a " 28

[1] E = *Euglossa*

[2] Date arrived at by comparative size of larva when examined February 4 and 5.

times. Despite these attacks the larva was still capable of movement. When next examined at 6:20 P.M. the larva was immobile and partially covered with dark wax; the *Stelis* was motionless on the side of the box. The cell from which the larva had been removed was still open at 7:10 A.M. the following morning but was being closed at 12:15 P.M. During the morning she opened another cell (sealed 6 days earlier) and removed and destroyed the tiny larva. This cell was still unsealed in the evening but was closed by 7:15 A.M. the following day (January 27). At midday no change was noted but at 4:15 P.M. a cell sealed on January 24 was opened and the egg removed; by 7:00 P.M. it was resealed. During the night the partially provisioned cell was sealed by *Stelis*, with material obtained from the tops of other cells. Whereas the other cells when resealed by the *Stelis* were nearly identical in appearance to unopened ones, the walls of this cell were shorter but the cell top was similar in shape to the others. All of the newer cells were near one end of the cell mass. During the next few days *Stelis* added wax to their tops, some of it obtained from the older cells and some from the wax seal along the edges of the box. No other cells were open during periodic inspection over the next several days. The female was present in the

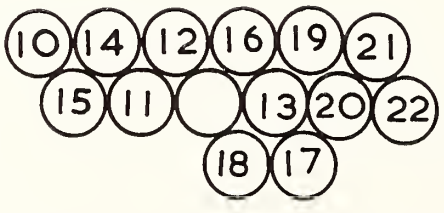

FIG. 2. Diagram of nest 9. Numbers refer to the order in which cells were provisioned by *Euglossa* female. Unnumbered cell was abandoned and capped by an earlier female. Table 2 provides pertinent data on the activities of the *Euglossa* and *Stelis* females.

Fig. 3. First-stage larva of *Stelis bilineolata* on provision mass in cell of *Euglossa cordata*. (Photo by J. Rozen.)

Fig. 4. Cocoon of *Stelis bilineolata*. (Photo by J. Rozen.)

box every morning and evening but was out at midday on January 28, 29, and February 1, returning before 1:15 P.M. each day. She was removed from the nest on February 4 when the cells were opened for observation of the feeding habits of the larvae.

Seven cells when opened contained fully fed larvae, prepupae, and pupae of *Euglossa*; all were dead except one prepupa (Table 2 and Figs. 1 and 2). Each of the other six, including the one which had not been completed by *Euglossa*, contained a single developing larva of *Stelis*.

DEVELOPMENT OF THE IMMATURE STAGES OF *Stelis*

The number of observations are inadequate for specific information on the duration of all of the immature stages. The egg which is laid on top of the cell provisions hatches 3 to 4 days after deposition; larval feeding is completed in 9 to 12 days; construction of the cocoon which commences shortly thereafter requires at least 3 days. The duration of the postfeeding larval and pupal stages was not recorded but the period from oviposition to adult emergence is approximately 60 days, i.e., about 7 to 10 days longer than that for *Euglossa*.

The feeding activities of larvae of varying ages were observed. The small

first-stage larva (Fig. 3) appears to be almost sedentary, moving only slightly on the surface of the viscous pollen–nectar mass. The body is only slightly curved dorsoventrally with its ventral surface in contact with the food. Half-grown and larger larvae lie on their backs while feeding, i.e., the dorsal part of the head and succeeding segments in contact with the food and with the posterior of the body towards the top of cell.

Defecation commences at least 48 hours before the provision mass is entirely consumed. The feces are in the form of elongate pellets narrowed at either end. They are from eight to ten times as long as broad with the first pellets smaller and attached lightly to the upper cell wall. Although the pellets are usually flattened by subsequent movements of the larva, the outline of many of the individual pellets can be readily seen in old cells. The feces are deposited in a broad belt on the upper part of the cell wall, some of them adhering to the cell top or dropping to the lower part of the cell. Defecation is completed before construction of the cocoon begins.

The completed cocoon (Fig. 4) is cylindrical with rounded bottom and a top that ends in an extruding nipple. It consists of several layers. First, a number of fine silken strands attached to the cell wall and feces are formed; this is followed by a parchment-like layer which follows the inner contours of the cell except at the top. The nipple protrudes into a depression at the top of the cell, the outer silken threads being more abundant than in the main section of the cell. Although the tip of the nipple normally adheres to the cell top, it is formed even if the top of the cell is removed prior to construction of the cocoon. The outer parchment is followed by a layer of loosely packed silken threads somewhat lighter in color; a further parchment layer which is a lighter golden brown and very smooth on its inner surface completes the cocoon. The inner surface of the top of the cocoon is rounded and quite smooth with no internal indication of the nipple. The silk of the cocoon is pale, almost transparent, as it leaves the salivary opening but later darkens to a golden brown.

The emerging adult chews an irregular, somewhat circular hole through the upper wall of the cocoon and cell.

The cocoon in shape and texture is strikingly similar to that of a small unidentified Trinidadian anthidiine and has a similar nipple-like protrusion. Furthermore, defecation in this species occurs before the cocoon is completed, suggesting that these activities among the parasitic group have not changed markedly from the nonparasitic anthidiines.

DISCUSSION

Although the association of the subgenus *Odontostelis* and *Euglossa* has been known for some time (Friese, 1925), details of the activities of the *Stelis* female in the host nest, particularly the opening of cells and the removal of the *Euglossa* eggs and larvae, have not been reported previously.

The behavior in the latter nest from which the host was driven out and did not return is the more usual because in four other nests which *Stelis* invaded the *Euglossa* adult when driven out never returned. Therefore, the behavior of the bee in the first nest may be considered uncharacteristic; her actions prior to the invasion of *Stelis* suggests parasitism by a conopid. As adults attacked by this parasite usually remain in the nests this would explain her "atypical" behavior in the presence of *Stelis*.

The habit of closing the entrance when entering and leaving the hosts' nest must also be relatively rare among parasitic bees. Also the behavior of the female in the nest, leaving and returning on several successive days, indicates that *Stelis* has retained many of the habits of the nonparasitic species.

Observations indicate that the *Stelis* female without opening a cell can detect whether it is suitable for the development of its young. The dissection of unparasitized cells shows no evidence of having been opened and reclosed when found unsuitable. This is evidence that the *Stelis* female is able to kill the large larvae, pupae, and even unemerged adults either by stinging or by squeezing the cell walls because in none of the nests attacked by *Stelis* did adults of *Euglossa* emerge subsequently. Furthermore, dissection of cells which failed to emerge revealed dead large larvae, prepupae, pupae, or adults of *Euglossa*. Although one live prepupa was found when the cells of nest 9 were examined the *Stelis* had not yet abandoned the nest.

Destruction of mature larvae and pupae in cells unsuitable for the development of her own progeny represents the destruction of potential hosts for successive generations which, on the basis of present observations, appears to be an undesirable trait. However, we do not know the reaction of an emerging *Euglossa* female towards parasitized cells; it is possible that she would sense their presence and either open the cells and destroy their contents or effectively block their emergence by the addition of more wax. If either were likely to occur then the destruction of *Euglossa* pupae and mature larvae would be of definite survival value to her own progeny and to the species.

Acknowledgments

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